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Kathryn A. Yurkonis
Iowa State University

Brian J. Wilsey
Iowa State University, bwilsey@iastate.edu

Kirk A. Moloney
Iowa State University, kmoloney@iastate.edu

Pauline Drobney
United States Fish and Wildlife Service

Diane L. Larson
United States Geological Survey
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Keywords

broadcast seeding, drill seeding, grassland restoration, heterogeneity, invasion, reconstruction, slot seeding, spatial pattern, tallgrass prairie

Disciplines

Ecology and Evolutionary Biology | Other Ecology and Evolutionary Biology | Terrestrial and Aquatic Ecology

Comments

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RESEARCH ARTICLE

Seeding Method Influences Warm-Season Grass Abundance and Distribution but not Local Diversity in Grassland Restoration

Kathryn A. Yurkonis,^{1,2} Brian J. Wilsey,¹ Kirk A. Moloney,¹ Pauline Drobney,³ and Diane L. Larson⁴

Abstract

Ecological theory predicts that the arrangement of seedlings in newly restored communities may influence future species diversity and composition. We test the prediction that smaller distances between neighboring seeds in drill seeded grassland plantings would result in lower species diversity, greater weed abundance, and larger conspecific patch sizes than otherwise similar broadcast seeded plantings. A diverse grassland seed mix was either drill seeded, which places seeds in equally spaced rows, or broadcast seeded, which spreads seeds across the ground surface, into 24 plots in each of three sites in 2005. In summer 2007, we measured species abundance in a 1 m² quadrat in each plot and mapped common species within the quadrat by recording the most abundant species in each of 64 cells. Quadrat-scale diversity and weed abundance

were similar between drilled and broadcast plots, suggesting that processes that limited establishment and controlled invasion were not affected by such fine-scale seed distribution. However, native warm-season (C₄) grasses were more abundant and occurred in less compact patches in drilled plots. This difference in C₄ grass abundance and distribution may result from increased germination or vegetative propagation of C₄ grasses in drilled plots. Our findings suggest that local plant density may control fine-scale heterogeneity and species composition in restored grasslands, processes that need to be further investigated to determine whether seed distributions can be manipulated to increase diversity in restored grasslands.

Key words: broadcast seeding, drill seeding, grassland restoration, heterogeneity, invasion, reconstruction, slot seeding, spatial pattern, tallgrass prairie.

Introduction

The arrangement of seeds in space may strongly affect the ways newly established communities develop in time. This is an important aspect to consider when planning a restoration where several methods are available for incorporating seeds into a landscape (Wilson 2002). Seed arrangement may have unintentional and long-lasting effects on restoration success (Allison 2002; Bartha et al. 2004) as a result of potential interactions that determine which species persist and their subsequent spatial arrangement (Stoll & Prati 2001; Monzeglio & Stoll 2005; Korner et al. 2008). Although theory predicts the distribution of seeds during establishment may influence fine-scale heterogeneity and species diversity (reviewed in Tilman & Kareiva 1997; Bolker et al. 2003), studies have mostly

considered this question in low-diversity, annual systems (e.g., Stoll & Prati 2001; Lortie et al. 2005; Monzeglio & Stoll 2005). Only a few studies (De Luis et al. 2008; Yurkonis et al. in press) have asked whether the initial spatial arrangement of seeds is related to subsequent vegetation structure in species-rich perennial systems. Here, we ask whether plant community structure, as measured by species diversity, composition, and fine-scale plant distribution, differs between replicated drill and broadcast seeded grassland plots. Our goal in this study is to investigate possible mechanisms that control grassland establishment and fine-scale heterogeneity.

Drill and broadcast seeded restorations differ in depth and distribution of seeds at planting and provide an interesting ecological context in which to study the effects of manipulating seed distributions in space. In drill seeded restorations, seeds are planted in equally spaced rows with short distances between neighboring seeds and large, uniform spaces between rows (Bufton 1978). In broadcast seeded restorations, seeds are dispersed across the soil surface with potentially longer and more variable distances between neighboring seeds (Packard & Mutel 1997; Skinner 2005). Only a handful of studies have systematically compared these seeding techniques for grassland restoration and have yielded mixed, often site-specific,

¹ Iowa State University, Department of Ecology, Evolution, and Organismal Biology, 253 Bessey Hall, Ames, IA 50011, U.S.A.

² Address correspondence to K. A. Yurkonis, email yurkonis@iastate.edu

³ United States Fish and Wildlife Service, Neal Smith National Wildlife Refuge, PO Box 399, 9981 Pacific Street, Prairie City, IA 50228, U.S.A.

⁴ United States Geological Survey, Northern Prairie Wildlife Research Center, 100 Ecology Building, 1987 Upper Buford Circle, St. Paul, MN 55108, U.S.A.

results. Montalvo et al. (2002) found increased establishment of large-seeded species in drilled coastal sage scrub and Sheley et al. (2006) found higher density of grasses in drilled pothole wetlands. In semiarid grasslands, Bakker et al. (2003) found lower seedling survivorship in drilled plantings. These studies have been important in understanding potential effects of planting method on recruitment, but because they did not consider diversity and fine-scale heterogeneity, we are unable to evaluate the long-term consequences of using either method.

There are several ways in which differences in planting method and subsequent seed arrangement may irreversibly affect plant community structure. Increased seeding depth (typically 1–2 cm) associated with drilling is predicted to favor grass germination (Redmann & Qi 1992). Initial seed distributions may also affect species composition and diversity (richness and evenness) through interactions among neighbors. In establishing grasslands, survival of neighboring seedlings was most influenced by neighbors within a 3-cm distance (Milbau et al. 2007). Seedlings of strong competitors (Stoll & Prati 2001; Lortie et al. 2005; Monzeglio & Stoll 2005) or early emerging seedlings (Korner et al. 2008) are most likely to persist among such relatively close neighbors. If reducing neighbor distance lowers overall establishment and favors competitive dominants without affecting overall germination, then drilled plantings with shorter mean nearest-neighbor distances should be less diverse than otherwise similar broadcast plantings.

Planting method may also affect how plants establish in space, a potentially important determinant of local resource uptake (De Boeck et al. 2006) and invasibility (Bergelson et al. 1993). Competitive exclusion of close neighbors may result in the formation of a few large conspecific patches, whereas greater distances among neighbors may result in more numerous and smaller conspecific patches (Stoll & Prati 2001; Monzeglio & Stoll 2005; Skinner 2005). Differences in general patch size and distribution may then affect net resource uptake, where multiple small patches would more completely exploit local niche space (Spehn et al. 2000; De Boeck et al. 2006). Resulting patch size and distribution may also affect local vegetative spread (Yurkonis, unpublished data) and longer-term competitive exclusion (Bergelson et al. 1993; Racz & Karsai 2006). If initial conditions dictate plant distributions in this way, then drilled plantings with shorter nearest neighbor distances should have fewer, larger patches. Investigating this space–composition relationship would further our understanding of factors influencing fine-scale heterogeneity and can provide insight into why plantings often have lower fine-scale heterogeneity than reference sites (Allison 2002; Martin et al. 2005).

Finally, initial seed distribution may also affect recruitment from the local propagule pool. The distribution and proportion of open space in a community can affect invasion among establishing seedlings (Goldberg & Werner 1983; Bergelson 1990; Bergelson et al. 1993). Larger, more contiguous open spaces, as in drilled plantings, may facilitate establishment from the local propagule pool over smaller, more dispersed spaces, as in broadcast plantings (Goldberg & Werner 1983; Bergelson

et al. 1993; Milbau et al. 2007). In a single species experiment, weed recruitment was greater in plots with clumped versus random distributions of *Poa annua* (Annual bluegrass) due to differences in local litter accumulation between treatments (Bergelson 1990). Invasion may also be affected by the ways in which resident species are distributed because larger, single species patches may not use resources as completely and are thus more susceptible to invasion (Tilman et al. 1996; Naeem et al. 2000). If this effect of neighbor distance and patch size on invasion is important in grassland establishment, then drilled plantings with large, uniform spaces between rows and potentially larger patches of resident species should have a greater proportion of nonsown species than broadcast plantings at comparable overall planting densities.

Drill and broadcast seeded grasslands may differ from one another as a result of initial differences in seeding depth, the proximity of nearest-neighbors, and the distribution of available sites for establishment of nonseeded species. However, to what extent these factors may affect grassland establishment in this context is unknown. A previous study (Yurkonis et al. in press) in two separately managed tallgrass prairie reconstruction sites found that the relative abundance and distribution of exotic species in one site and native warm-season grasses in a second site were greater in drilled plantings, suggesting that the distribution of seeds and open sites in plantings may control fine-scale heterogeneity and local invasion. Yurkonis et al. (in press) found site-specific effects of seeding method which may be attributable to differences in seed mix composition or site management among other factors. This study expands upon our previous work by comparing vegetation structure in replicated drilled and broadcast seeded plots in a multisite study to determine whether there are consistent differences between these seeding methods across similarly managed sites.

We sampled replicated plots in a multisite study on grassland restoration to address the question: Are there differences in vegetation structure between drilled and broadcast seeded grasslands several years after planting? We test the hypotheses that in drilled plots (1) species diversity will be lower due to decreased establishment among close neighbors; (2) weeds (nonplanted native and exotic species) will be more abundant due to larger more contiguous spaces among rows of establishing seedlings; and (3) strong competitors will occur in larger and more contiguous patches. Although controlled experimental studies are still needed to directly test the mechanisms structuring these communities, spatially explicit comparative data allows us to make further testable predictions about the mechanisms structuring restored grasslands.

Methods

Study Site

Experimental plots (Thistle Suppression Research Plots) were planted in 2005 at Neal Smith National Wildlife Refuge (NSNWR; U.S. Fish and Wildlife Service, Prairie City, Iowa; lat 41°33'N, long 93°16'W) to examine the effects different

planting methods may have on grassland restoration success. NSNWR is located on the southern Iowa drift plain where the mean annual temperature is 9.4°C and the mean annual precipitation is 836 mm. Three sites within the refuge were each planted with 12 replicate (12.2 × 12.2 m) plots of 12 seeding and diversity treatments in a full factorial design. All three sites, Production, Orbweaver, and Harmison, were in annual crop production the year before planting and were treated with herbicide (glyphosate and 2,4-D) prior to planting. Soils are relatively consistent within sites, but do vary among sites. The soils of the Production site are predominantly Aquertic Argiudolls, the soils of Orbweaver are mostly Oxyaquic Argiudolls, and the soils of Harmison are primarily Mollic Hapludalfs (Nestrud & Woster 1979). Production and Orbweaver soils formed in loess; however, Harmison soils formed in glacial till.

In July 2007, we sampled spring planted (2005), medium-diversity, drilled and broadcast plots (2 seeding treatments × 12 replicates × 3 sites = 72 plots) within the Thistle Suppression Research Plots. These plots were either drill seeded or broadcast seeded (430 seeds/m²) with a 20 species seed mix (Table 1) where 70% of the seeds (by numbers) were grasses and 30% forbs, a ratio commonly used in large-scale plantings throughout the region (but not at NSNWR). Plots

were either drill seeded with a Tye seed drill (Lockney, TX, U.S.A.; 20.32 cm spacing between rows) or broadcast with a Vicon broadcast seeder (Cotia, Brazil). The mix contained 13 forbs and 7 grasses with *Elymus canadensis* (Canada wildrye) seeded in a higher proportion (20%) than the remaining grasses (Table 1). Pure live seed was purchased from Allendan Seed Company in Winterset, Iowa and mixed on site. All plots were mowed once in 2005 and 2006 and have not been burned.

Vegetation Sampling

Plant community structure was measured in a 1 m² quadrat randomly located to the north of the central marker in each plot (see Yurkonis et al. in press for further sampling details). All species were recorded and species relative abundance measured through point intercept sampling within a 1 m² sampling frame placed over each quadrat (Jonasson 1988). We recorded the identity of every leaf and stem touched by each of 40 pins dropped uniformly across the quadrat. A small value (0.5 touch) was added for each species that was present but was not touched by a pin when calculating diversity measures. Species relative abundance was determined by dividing the total touches for species *i* in a quadrat by the total touches in the quadrat. These data were used to determine planted species

Table 1. The number of quadrats containing each planted species in three sites, Harmison (HR), Orbweaver (OW), and Production (PP), of a study on drill and broadcast seeding in Iowa, U.S.A.

Species ^a	Common Name	HR	OW	PP
Grasses				
<i>Andropogon gerardii</i>	Big bluestem	20	21	22
<i>Bouteloua curtipendula</i>	Sideoats grama	21	17	15
<i>Elymus canadensis</i>	Canada wildrye	24	22	24
<i>Elymus virginicus</i> ^b	Virginia wildrye	1	1	—
<i>Panicum virgatum</i>	Switchgrass	12	13	16
<i>Sorghastrum nutans</i>	Indian grass	16	12	13
<i>Sporobolus asper</i>	Rough dropseed	5	7	1
<i>Schizachyrium scoparium</i>	Little bluestem	4	5	4
Legumes				
<i>Dalea candida</i>	White prairie clover	2	1	4
<i>Dalea purpurea</i>	Purple prairie clover	2	—	—
<i>Lespedeza capitata</i>	Round-headed bush clover	6	—	—
Forbs				
<i>Aster novae-angliae</i>	New England aster	22	7	7
<i>Chamaecrista fasciculata</i> ^b	Partridge pea	2	—	1
<i>Helianthus occidentalis</i>	Fewleaf sunflower	1	2	4
<i>Heliopsis helianthoides</i>	Smooth oxeye	2	2	6
<i>Monarda fistulosa</i>	Wild bergamot	1	6	8
<i>Rudbeckia hirta</i> ^b	Blackeyed Susan	6	4	3
<i>Echinacea pallida</i> ^b	Pale purple coneflower	—	1	—
<i>Solidago rigida</i>	Stiff goldenrod	1	1	1
<i>Solidago speciosa</i> ^b	Showy goldenrod	—	1	—
<i>Tradescantia ohiensis</i> ^b	Ohio spiderwort	—	—	1
<i>Verbena stricta</i>	Blue vervain	1	—	—
<i>Zizia aurea</i>	Golden Alexander	12	2	10

In each site, a 1 m² quadrat was sampled in each of 24 plots. Of the 20, 17 species in the seed mix and five species planted in additional treatments in the study were recorded. ^a *Artemisia ludoviciana* (Prairie sage), *Coreopsis palmata* (Prairie coreopsis), and *Potentilla arguta* (Prairie cinquefoil) were included in the seed mix, but were not present in the sampled quadrats.

^b Species that were not included in the 20 species seed mix but were seeded elsewhere in the study.

richness (S), Simpson's diversity ($1/D$), where $D = \sum p_i^2$ and p_i = relative abundance of species i , and evenness ($[1/D]/S$) at the quadrat-scale (Wilsey et al. 2005).

We used a cell-based approach (Herben et al. 1993) to quantify plant distributions in each quadrat. Each quadrat was divided into sixty-four 12.5×12.5 cm cells with metal rods passed through holes in the quadrat frame. This cell size corresponds to the average plant density in a remnant tall-grass prairie (Losure et al. 2007), and thus was an appropriate scale to capture individual plants. We recorded the species occupying 50% or more of the aboveground space in each cell. This method generated a fine-scale map of the species throughout the quadrat used in patch-based analyses with the program QRULE (Gardner 1999; Gardner & Urban 2007). A patch was defined as a group of neighboring conspecific cells (12.5×12.5 cm) where the four cells immediately adjacent to and the four cells on the diagonal from a focal cell were considered neighboring cells (Turner et al. 2001). With these data, we computed several simple metrics of landscape composition: number of species per map, proportion of the quadrat covered by a focal species, mean patch area, and patch mean-squared radius (see Yurkonis et al. in press for descriptions). Patch mean-squared radius is a measure of within patch dispersion in meters, where larger mean-squared radius values indicate that a larger area is needed to encompass the patch (Gardner 1999).

As with Yurkonis et al. (in press), we assessed plant distributions in two ways within each quadrat. First, we calculated mean patch size (m^2) and within patch dispersion (m) across *all* patches within each quadrat, irrespective of their species occupancy. Second, we determined the proportion of the quadrat covered by native warm-season (C_4) grasses and the mean size and dispersion of C_4 patches. C_4 grasses were of particular interest because they can dominate restorations despite efforts to promote realistic native species composition (Sluis 2002; Derner et al. 2004; Martin et al. 2005). For the C_4 grass analysis, each quadrat map was simplified into two classes, native warm-season grass and "other," and then summarized via QRULE. Quadrats that did not include C_4 grasses were not included in analyses of C_4 grass distributions, as seeds may not have been dispersed into these locations at planting. Although the first analysis tested for differences in general patch structure, the second analysis tested whether the dominant functional group in this system occupied space, and potentially used resources differently between plantings.

Photosynthetically active radiation (PAR) captured by the canopy was also measured within each quadrat using a Decagon AccuPAR LP-80 sensor light meter (Pullman, WA, U.S.A.) for the below canopy measurement and a Li-Cor external point sensor (Lincoln, NE, U.S.A) for the above canopy measurement. Above and below canopy midday (10–2 CST) PAR was measured twice, in a North–South and East–West direction, within each quadrat and the results averaged. From the PAR data, we determined the percentage of available light captured (1 minus % PAR at soil surface) as a proxy for overall resource capture. We also calculated the variance to mean ratio, a simple measure of spatial heterogeneity (Dale et al.

2002), for each light reading (a series of 80 measurements) to test whether differences occurred between planting types in the spatial heterogeneity of light capture.

Data Analysis

We used multivariate and univariate analysis of variance (MANOVA/ANOVA; PROC GLM; SAS Version 9.1; SAS Institute, Inc.) to test for quadrat-scale differences in planted species diversity, composition, plant distributions, and light capture between drilled and broadcast quadrats. Multivariate tests were based on the Wilk's λ test statistic and were used to test for overall effects among diversity and spatial parameters. Species relative abundances were arcsine square root transformed and patch size and mean-squared radius data were log transformed to meet normality assumptions. Two quadrats (one drilled and one broadcast) in Orbweaver were not included in the final analyses because they had no established planted species. We report type III sums of squares for the C_4 grass distribution analysis because the number of drilled and broadcast quadrats containing C_4 grasses was unequal within each site. The analysis model included site, planting type and site \times planting type as fixed factors tested with the residual quadrat error term. With this analysis, we assessed differences between plantings within these specific reconstructions.

Results

Although there were significant differences in the magnitude of some responses among sites, there were consistent treatment effects across sites and no significant treatment by site interactions for any of the analyses.

Planted Species Diversity

Individuals from 17 of the 20 species in the seed mix and from five species seeded elsewhere in the site were recorded in at least one of the quadrats. However, quadrat-scale diversity did not reflect that of the seed mix. Only five species (all grasses) were consistently present in more than half of the quadrats (Table 1) and approximately one-quarter of the planted species were present in any given quadrat. There was no effect of planting type on Simpson's diversity, species richness, or evenness and no overall effect of planting type on these diversity measures (Table 2; Fig. 1). Planted species Simpson's diversity and evenness differed among sites and there was an overall effect of site on diversity (Table 2; Fig. 1).

Species Composition

Although planted species richness was low compared to that of the seed mix, more than 75% of the leaf hits were from native planted species (Fig. 2). Quadrats were primarily comprised of *Elymus canadensis* that was seeded as a cover crop with the seed mix. The most common

Table 2. F-values from univariate and multivariate (based on the Wilk's λ test statistic) ANOVA of quadrat-scale Simpson's diversity (1/D), species richness (SR), and evenness (E) in replicate drilled and broadcast grassland plantings in Iowa, U.S.A.

Source	df	1/D	SR	E	df	Wilk's λ	F
Site (S)	2	13.41***	1.61	8.54***	6.124	0.616	5.63***
Planting type (P)	1	3.24 [‡]	3.69 [‡]	0.08	3.62	0.908	2.31 [‡]
S \times P	2	0.30	0.04	0.11	6.124	0.988	0.13
Error	64						

[‡] $p < 0.10$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

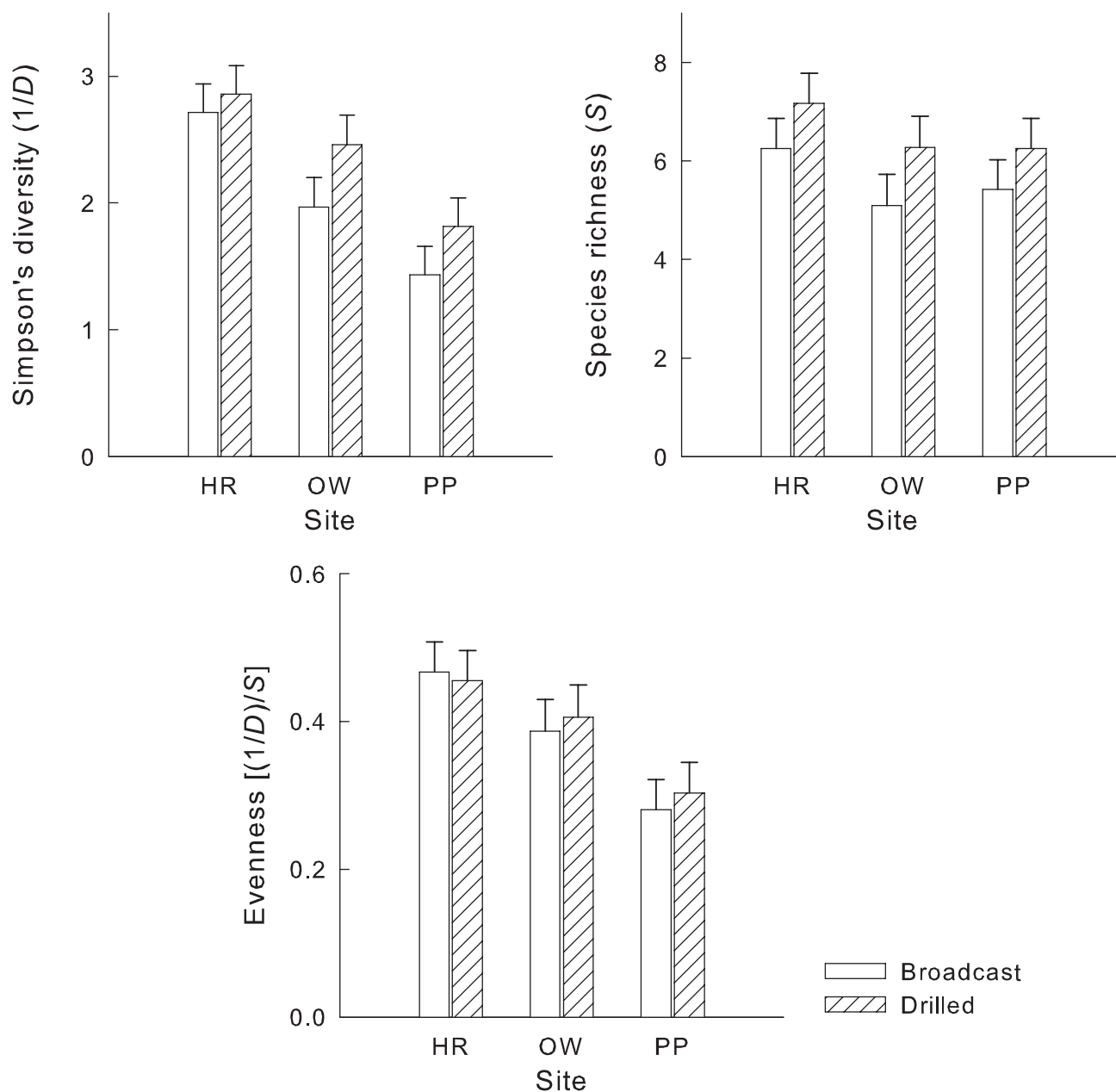


Figure 1. Quadrat-scale planted species diversity (Simpson's diversity, evenness, and species richness) for broadcast and drilled plots in three sites, Harmison (HR), Orbweaver (OW) and Production (PP) at Neal Smith National Wildlife Refuge, Iowa, U.S.A. Means are shown ± 1 SE from ANOVA.

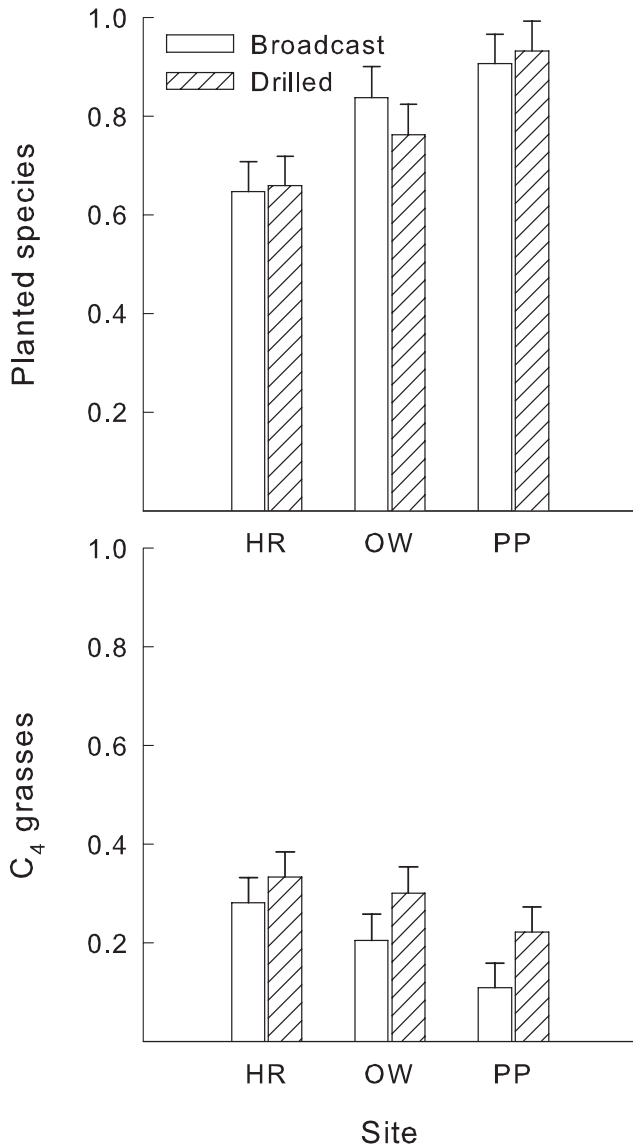


Figure 2. Species relative abundance in broadcast and drilled quadrats across three sites at Neal Smith National Wildlife Refuge, Iowa, U.S.A. Means are shown ± 1 SE from ANOVA with untransformed data.

nonsown species were the exotic *Setaria viridis* (Green bristlegrass) and the native *Conyza canadensis* (Canadian horseweed). Weed species abundance, the combined abundance of nonplanted native species and exotic species, differed

among sites ($F_{[2,64]} = 10.85$; $p < 0.001$), but was similar between planting types (Fig. 2; $F_{[1,64]} = 0.02$; $p > 0.05$; Site \times Planting type, $F_{[2,64]} = 0.33$; $p > 0.05$). Native warm-season grasses, which included *Andropogon gerardii* (Big bluestem), *Panicum virgatum* (Switchgrass), *Schizachyrium scoparium* (Little bluestem), *Bouteloua curtipendula* (Sideoats grama), and *Sorghastrum nutans* (Indian grass), were equally abundant among sites ($F_{[2,64]} = 2.44$; $p = 0.10$) and more abundant in drilled quadrats (Fig. 2; $F_{[2,64]} = 4.58$; $p < 0.05$; Site \times Planting type, $F_{[2,64]} = 0.53$; $p > 0.05$).

Plant Distribution

The number of species recorded within quadrat maps, mean patch size, and mean patch mean-squared radius differed among sites, but were similar between planting types (Table 3; Fig. 3). Native warm-season grasses occupied space in different ways among sites and between drilled and broadcast quadrats (Table 4; Fig. 3). Although there was no overall effect of planting type on warm-season grass distribution, there were significant effects of planting type in the univariate tests. Drilled quadrats contained a greater proportion of C₄ grass attributed cells and more dispersed patches over broadcast quadrats (Table 4; Fig. 3).

Resource Use

There was no effect of planting type ($F_{[1,64]} = 2.65$, $p > 0.05$) or site ($F_{[2,64]} = 2.94$, $p > 0.05$; site \times planting type: $F_{[2,64]} = 0.04$, $p > 0.05$) on mean light uptake (Fig. 4). In addition, there were no differences in the variance to mean ratio among sensors in each light measurement between treatments ($F_{[1,64]} = 0.14$, $p > 0.05$), but there was among sites ($F_{[2,64]} = 3.17$, $p < 0.05$; Site \times Planting type: $F_{[2,64]} = 0.06$, $p > 0.05$).

Discussion

We compared drilled and broadcast seeded grassland plots, which vary in seeding depth and spatial arrangement of seeds at planting, to identify whether and how initial planting method may influence grassland establishment 2 years after planting. As with Yurkonis et al. (in press), we found that planting method did not affect quadrat-scale Simpson's diversity, species richness, or evenness in these young plantings. We also found that weed relative abundance was similar between

Table 3. F-values from univariate and multivariate (based on the Wilk's λ test statistic) ANOVA of quadrat-scale plant distribution metrics (map species richness, mean patch size, and patch mean-squared radius) in replicate drilled and broadcast grassland plantings in Iowa, U.S.A.

Source	df	Map SR	Size (m ²)	Dispersion (m)	df	Wilk's λ	F
Site (S)	2	8.84***	25.25***	5.27**	6,124	0.499	2.29*
Planting type (P)	1	0.99	0.80	0.00	3,62	0.955	0.88
S \times P	2	0.31	0.84	0.46	6,124	0.944	1.21
Error	64						

Mean patch size and patch mean-squared radius (dispersion) were log transformed to improve normality.

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

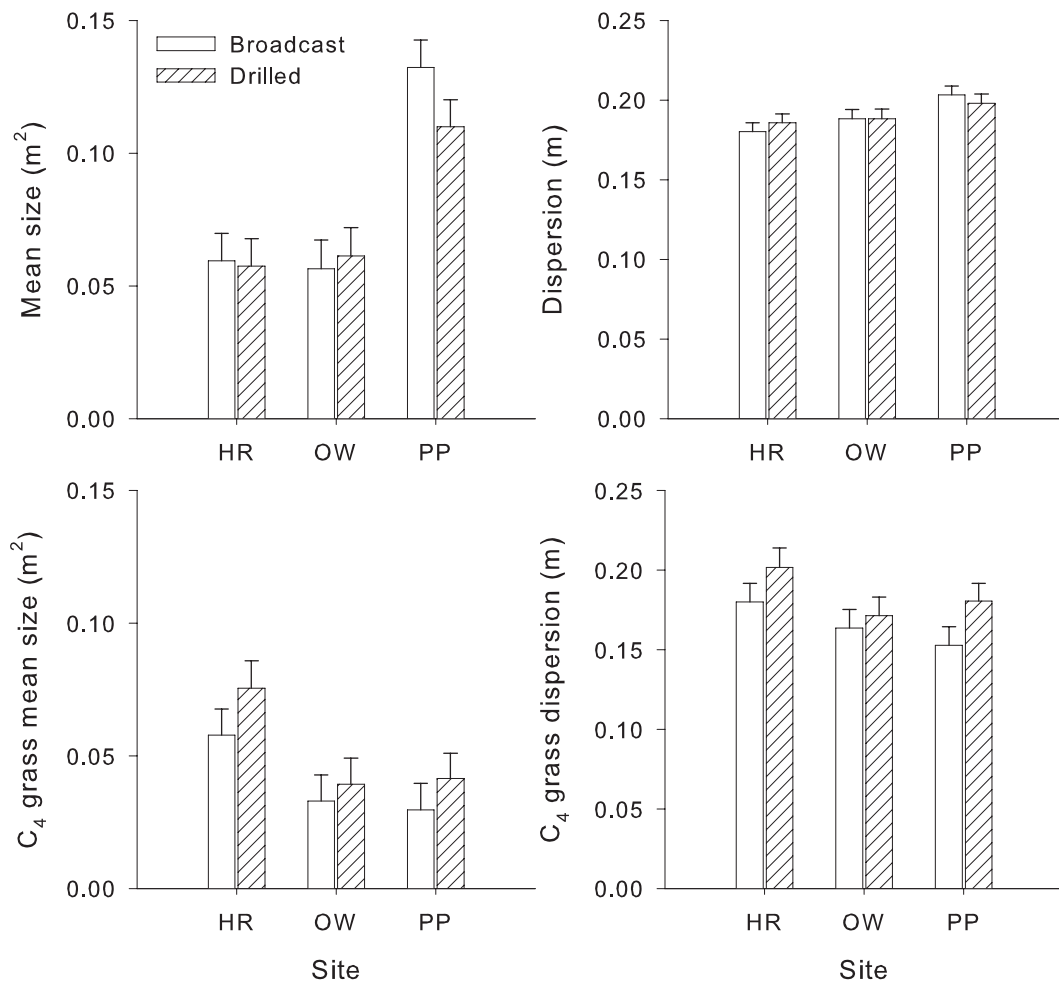


Figure 3. Mean patch size and dispersion across all species within sample quadrats and of native warm (C_4) season grass patches in broadcast and drilled plots in three sites at Neal Smith National Wildlife Refuge, Iowa, U.S.A. Means are shown ± 1 SE from ANOVA with untransformed data.

Table 4. F-values from univariate and multivariate (based on the Wilk's λ test statistic) ANOVA of quadrat-scale native warm-season (C_4) grass distribution metrics in replicate drilled and broadcast grassland plantings in Iowa, U.S.A.

Source	df	Proportion	Size (m^2)	Dispersion (m)	df	Wilk's λ
Site (S)	2	6.23**	4.70*	2.42 [‡]	6,116	2.40*
Planting type (P)	1	4.39*	3.15 [‡]	4.27*	3,58	1.69
S \times P	2	0.12	0.0016	0.28	6,116	0.61
Error	60					

Analyses were limited to plots where a warm-season grass was recorded in at least one cell. Mean patch size and patch mean-squared radius (dispersion) were log transformed to improve normality.

[‡] $p < 0.10$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

quadrats in drilled and broadcast seeded plots. These results suggest that the processes regulating species establishment and invasion were not affected by altering fine-scale seed distributions, and we conclude that, from a management perspective, drill and broadcast seeding are interchangeable in this regard.

Theory predicts that interactions should be more intense among close individuals in establishing communities (reviewed in Tilman & Kareiva 1997; Bolker et al. 2003), such that

communities that differ in initial seed arrangement should differ in composition and diversity. However, our findings suggest that changing seed distributions while maintaining coarser-scale planting density did not affect overall species establishment and subsequent diversity. There are several potential causes for this outcome. The effects of aggregating seeds into rows in drilled plots may have been offset by seed movement along the ground surface after planting (Harper et al. 1965) or seedlings growing into the large open

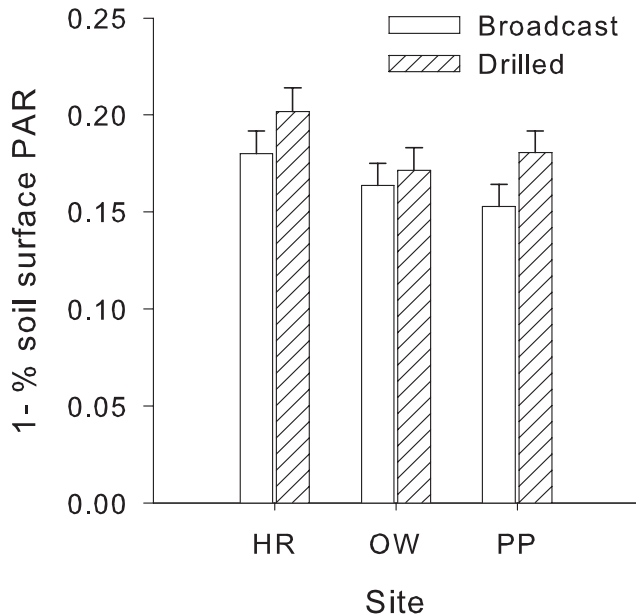


Figure 4. Quadrat-scale mean canopy light capture for broadcast and drilled plots in three sites at Neal Smith National Wildlife Refuge, Iowa, U.S.A. Means are shown ± 1 SE from ANOVA.

spaces between rows (Coulson et al. 2001). Seed density may also have been low enough that seeds were placed far enough apart as not to be influenced by establishing neighbors (Milbau et al. 2007) in both treatments, although 430 seeds/m² is greater than most recommended seed densities (Packard & Mutel 1997; Wilson 2002). Finally, germination may have been higher in drilled plots which could offset any effect of aggregation on competitive exclusion in drilled plots. In a separate greenhouse study, seedling density was greater in simulated drilled plantings than in simulated broadcast plantings seeded at 3940 seeds/m² (Yurkonis, unpublished data), probably due to increased germination with greater seeding depth (Redmann & Qi 1992). This difference persisted to the end of the first growing season as the number of individuals declined due to thinning. More seedlings were competitively excluded in the drilled treatment, but the outcome of thinning was similar between treatments. Species diversity, richness, and evenness were similar between drill and broadcast seeded treatments at the end of the study (Yurkonis, unpublished data). In this study, thinning may also have affected species equally between drilled and broadcast plantings. Unfortunately, we were unable to measure seedling density at the start of the experiment, so we leave future studies to test among these scenarios of seedling interactions.

Generally, species establishment from the seed mix was low in both types of plots. We used a seed mix with a high proportion of grasses which may have outcompeted forb seedlings in the establishing plantings (Packard & Mutel 1997). However, increasing the percentage of forbs did not result in an increase in species richness in an additional seeding treatment in this study (Larson, unpublished data). Other factors that could affect species establishment equally

between planting types include season of planting (fall versus spring) and seed predation (Packard & Mutel 1997; Wilson 2002). Future studies need to control for such factors that limit overall establishment to test the role that changing distances among neighboring seeds, while maintaining overall density, plays in establishing grasslands.

Exotic species and native nonplanted species were predicted to establish more frequently in the larger and more contiguous open spaces (Bergelson 1990; Bergelson et al. 1993) between rows in drilled plots. However, in this site there were no differences in weed abundance between drilled and broadcast plots. Thus far, previous studies have found mixed effects of drill versus broadcast seeding on species invasion. Sheley et al. (2006) found no effect of planting method on weed abundance when perennial grasses were drilled and broadcast into pothole wetlands. However, the introduced grass *Agropyron cristatum* (Crested wheatgrass) was occasionally more abundant when native species were drilled over broadcast into semiarid grasslands dominated by the grass (Bakker et al. 2003). Exotic species were more abundant in a drilled planting at a second site in the tallgrass prairie region and were similar in abundance between a drilled and broadcast planting in yet a third location under different management (Yurkonis et al. in press). Differences among sites in the response of weed species to planting methods may be attributable to differences in the size of the weed seed bank. Prior agricultural production in our sites likely reduced the weed seed bank to a few annual invaders (Menalled et al. 2001), which may have been quickly outcompeted by establishing perennials. In grasslands reconstructed in former agriculture fields, invaders may become more problematic over time (Naem et al. 2000; De Cauwer et al. 2005). In this case, fine-scale heterogeneity in the established vegetation may inhibit invasion and the effect of planting method on invasion may become more pronounced over time (but see Wilson 2002; De Cauwer et al. 2005).

Although other aspects of plant community structure were similar between seeding treatments, the dominant species in this system, native warm-season grasses, responded differently to drill and broadcast seeding. C₄ grasses were more abundant and occurred in less compact patches in drilled plots. The C₄ grasses were not present prior to planting due to the long history of annual crop production at these sites and had to have established from seed. Germination and resulting abundance may have been higher in drilled plots as a result of increased seeding depth (1 cm versus surface seeding in broadcast plots) (Redmann & Qi 1992). Differences in distribution may result from the aggregation of seeds during the drilling process, fine-scale seed movement due to differences in ground surface topography with drilling (Harper et al. 1965; Bufton 1978), or differences in vegetative propagation into unoccupied areas (Packard & Mutel 1997). Local microsites (e.g., soil characteristics) can also control establishment, but we would expect the same patterns between drilled and broadcast plots. Our findings support other nonspatial studies of drilled and broadcast plantings which have found higher survivorship (Bakker et al. 2003), biomass (Jackson 1999), and density (Sheley et al. 2006) of native grasses in drilled plantings.

Over time, C_4 grass abundance may increase in these plots (Sluis 2002; Derner et al. 2004) and their initial distributions may have long-term effects on local species turnover. C_4 grasses are maintained by vegetative propagation and fragmentation and can persist for multiple decades (Derner et al. 2004), although some species may be much more dynamic over shorter time scales (Herben et al. 1993). Because the dominant plants may be relatively stable in their positions through time, it is important to consider how distributions early in a restoration may affect local resource use and future species turnover. Benson and Hartnett (2006) found that in a remnant grassland, most new individuals arise from vegetative recruitment from long-lived individuals as opposed to seedling establishment. Seedling recruitment is also likely limited in established grassland restorations, but further work is needed to investigate this question.

If local species turnover in restored communities is dictated by dominant long-lived individuals, such as C_4 grasses, then seedling distributions at establishment may affect future rates of competitive exclusion, resource use, and species turnover (Tilman 1993; De Boeck et al. 2006; Racz & Karsai 2006). C_4 grasses consume nutrients differently than C_3 grasses and forbs (Wedin & Tilman 1990). Thus, dispersed patches of C_4 grasses may affect local resource cycling more extensively than compact patches (Spehn et al. 2000; De Boeck et al. 2006). Differences in resource uptake associated with different plant distributions may then affect resources available for local colonization and alter invasibility and species turnover (Tilman 1993; Naeem et al. 2000). Although there were no differences in light use, a proxy for resource use, at these sites, similar older plantings did have differences in light uptake between drilled and broadcast plantings (Yurkonis et al. in press). Further testing is needed to determine present and long-term impacts of different plant distributions on resource dynamics.

Conclusions

By considering species diversity and fine-scale distribution in planning and assessing restorations, we can further our understanding of the mechanisms controlling community assembly in restored and natural systems. This application of spatial theory in restoration practice has been suggested for restoration of wild rice marshes (Liu et al. 2004), coral reefs (Sleeman et al. 2005), and plant communities in general (Bartha et al. 2004). Previous studies have shown that neighbor associations are important for determining local colonization (Goldberg & Werner 1983; Milbau et al. 2007) and extinction (Stoll & Prati 2001; Monzeglio & Stoll 2005; Racz & Karsai 2006) and that spatially dependent processes may be important for determining long-term community dynamics (reviewed in Tilman & Kareiva 1997). Our findings suggest that local plant density may control fine-scale heterogeneity in restored grasslands and demonstrate that species distribution is a potentially important factor to consider when initiating a restoration in sites that have been previously depleted of their native species pool (e.g., Muller et al. 1998; Walker et al. 2004). These methods need to be further investigated to determine whether local

density affects long-term resource use and diversity maintenance in these plantings and if fine-scale species distributions can be manipulated in other ways (e.g., through conspecific aggregation) to increase diversity in restored communities.

Implications for Practice

- Drill and broadcast seeding produce communities that are similar in diversity and weed abundance 2 years after planting.
- Drill seeding may result in greater abundance and more dispersed patches of dominant species than broadcast seeding. How these differences affect future diversity needs to be further investigated.
- Site characteristics strongly affect diversity and plant distribution in newly established grassland restorations. The effects of drill versus broadcast seeding are not altered by such differences among sites, although different management scenarios may produce different outcomes.

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